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BIOLOGICAL BULLETIN

NO CROSSING OVER IN THE MALE OF DROSOPHILA OF GENES IN THE SECOND AND THIRD PAIRS OF CHROMOSOMES.

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In a brief note in *Science* for November 22, 1912, it was pointed out that there was no "crossing over" in the male between the factors for black body color and vestigial wings, while between the same factors in the female there was 22 per cent. of crossing over. The data then published have been extended and revised,[1] and the results can now be given in detail. For purposes of easy comparison I shall present the data in the same order as those given in the preliminary report.

It had been shown by Morgan and Lynch (BIOL. BULL., XXIII., 1912) that when black flies having normal (long) wings are mated to gray flies having vestigial wings, only three classes appear in F_2, viz.:

Gray Long.	Black Long.	Gray Vestigial.	Black Vestigial.
4569	2151	1626	0

It was pointed out later (*Science*, 1912) that the absence of the black vestigial class would be expected, if, in F_1, no interchange of factors occurs in one sex. The following analysis will make evident why, on the assumption that there is no crossing over in the gametogenesis of the F_1 male, there are no black vestigials expected in F_2.

[1] We have learned better how to control the conditions of culture so that less disturbance results from differential viability. Many of the old data, although consistent within themselves, are not strictly comparable with the recent data obtained under better conditions. For the case of black and vestigial the data presented here differ from those reported (*Science*, 1912) in that new data have been substituted for some of the old data in the tests of the amount of crossing over in the female.

Black long ♀, bV_g—bV_g.
Gray vestigial ♂, Bv_g—Bv_g.

F_1 ♂ or ♀, bV_gBv_g.

Gametes of F_1 { BV_g—bV_g—Bv_g—bv_g Eggs
bV_g—Bv_g Sperm.

F_2 {
BV_g bV_g, gray long, BV_g Bv_g, gray long.
bV_g bV_g, black long, bV_g Bv_g, gray long.
Bv_g bV_g, gray long, Bv_g Bv_g, gray vestigial.
bv_g bV_g, black long, bv_g Bv_g, gray vestigial.

The expectation is 4 gray long, 2 black long, 2 gray vestigial, 0 black vestigial. The data show that the gray vestigial run behind expectation, which is due to viability (crowding out through competition). It is evident that the expectation would be the same if the failure to cross over occurred in the female instead of in the male as here assumed. In order to test which sex failed to give crossing over the following matings were made. (1) Black, long winged females were mated to gray, vestigial winged males. The F_1 flies ♂ and ♀ were gray, long. The F_1 males were bred to black vestigial females and gave *two* classes.

Gray Long.	Black Long.	Gray Vestigial.	Black Vestigial.
0	19	19	0
0	30	33	0
0	34	20	0
0	193	115	0
0	174	118	0
0	542	416	0
0	992	721	0

If we assume that there has been no crossing over in the F_1 heterozygous males the result is explicable, as shown in the following analysis, except in so far as the gray vestigials are crowded out.

Black vestigial ♀, bv_g—bv_g,
F_1 ♂, bV_g—Bv_g,

F_2 bv_g bV_g, black long,
bv_g Bv_g, gray vestigial.

The F_1 heterozygous females (sisters to the males just tested) were also tested by crossing to black vestigial males. *Four* classes were produced.

Gray Long.	Black Long.	Gray Vestigial	Black Vestigial.
66	283	201	58
65	243	224	50
55	218	169	42
20	113	112	29
71	311	210	47
17	153	181	20
44	231	218	48
338	1,552	1,315	294

This result, in contrast to the last one, is explicable on the assumption that crossing over occurs in the female, as the following analysis shows:

F_1 ♀, BV_g—bV_g—Bv_g—bv_g,
Black vestigial ♂, bv_g— bv_g

BV_g bv_g, gray long.
bV_g bv_g, black long.
Bv_g bv_g, gray vestigial.
bv_g bv_g, black vestigial.

The expectation on the basis of *free* crossing over in the female is 2 gray long, 2 black long, 2 gray vestigial, 2 black vestigial. The two classes gray long and black vestigial are cross over classes, and their smaller numbers result from linkage. It will be noted that the two vestigial classes fall below the corresponding long classes, and this can be accounted for as due to viability. The percentage of crossing over on the basis of the data is 17.9.

These last two experiments show that the realized classes are explicable on the basis of non-crossing over of factors in the heterozygous male, and of crossing over to the extent of 17.9 per cent. in the female. This conclusion can be tested by bringing into the cross the same factors in other combinations. One such test is as follows. Gray, long winged females (BV_g) were bred to black, vestigial males (bv_g) and produced gray long males and females. The F_1 heterozygous males produced in this way were mated to black vestigial females, and gave:

Gray Long.	Black Long.	Gray Vestigial.	Black Vestigial.
18	0	0	18
90	0	0	95
174	0	0	78
102	0	0	86
384	0	0	277

This result is what is to be expected on the basis of no crossing over in the heterozygous male as the following analysis shows:

Black vestigial ♀, bv_g—bv_g
F_1 ♂, BV_g—bv_g

bv_g BV_g, gray long.
bv_g bv_g, black vestigial.

The F_1 heterozygous females (sisters to the males just tested) were in turn mated to black vestigial males and gave:

Gray Long.	Black Long.	Gray Vestigial.	Black Vestigial.
255	55	47	184
163	24	37	139
47	9	11	33
121	18	16	109
586	106	111	465

These results are explicable if crossing over (17.1 per cent.) takes place in the F_1 heterozygous females, as indicated below:

F_1, bV_g—BV_g—bv_g—Bv_g
Black vestigial, bv_g—bv_g

bV_g bv_g, black long.
BV_g bv_g, gray long.
bv_g bv_g, black vestigial.
Bv_g bv_g, gray vestigial.

It has been pointed out that when the factors for black and for long wings go in together, *i. e.*, enter with the same chromosome, and the factors for gray and for vestigial enter with the other chromosome (it does not matter which parent contributes each) the double recessive does not appear in F_2. In more general terms it may be said, for the second chromosome, that when two recessives enter, one from each side, the double recessive does not

appear in the F_2 generation. The explanation of this is clear on an examination of the first analysis. Since there is no crossing over in the male, each gamete in the male will contain one or the other of the dominant factors, hence no double recessive zygote can appear, and every zygote must contain at least one dominant. This means that there is one class with two dominants, one with the one, one with the other. If we assume that the factors are carried by specific chromosomes, and that the factors for black and for vestigial (and hence for their normal allelomorphs) lie in the homologous chromosomes, we can explain the results just given on the basis that no interchange of factors occurs between these chromosomes in the male even though in the female interchange takes place. Why an interchange should take place in one sex and not in the other cannot be stated, but I should not be surprised if a thorough cytological study would throw some light on the subject.

The converse case is that of two recessives entering from the same side, in which case all the expected classes appear in F_2. An example with its analysis will make this clearer. Gray, long winged females (double dominants) were mated to black vestigial males (double recessives) and gave gray long winged F_1 offspring. These F_1 flies, mated, gave in F_2:

Gray Long.	Black Long.	Gray Vestigial.	Black Vestigial.
246	9	18	63

The following analysis shows why the result to be expected here is different from that in the last case. Half of the gametes

Gray long ♀, BV_g—BV_g.
Black vestigial ♂, bv_g—bv_g.

F_1 ♂ and ♀, BV_g—bv_g.

Gametes of F_1 bV_g—BV_g—bv_g—Bv_g Eggs
BV_g—bv_g Sperm

bV_g BV_g, gray long, bV_g bv_g, black long,
BV_g BV_g, gray long, BV_g bv_g, gray long,
bv_g BV_g, gray long, bv_g bv_g, black vestigial,
Bv_g BV_g, gray long, Bv_g bv_g, gray vestigial.

in the male contain both recessive factors and in consequence, even with no crossing over in the male, the realization of a double recessive zygote becomes possible.

The expected ratio without linkage in the female is 5 : 1 : 1 : 1. Four classes are expected and four appear, but the ratio given above is entirely changed by the linkage of the factors which here, on our assumption, lie in the same chromosome.

Purple Eyes and Vestigial Wings.

An eye color called purple also shows linkage with vestigial and is placed, therefore, in the second group of factors. It has likewise been used to test non-crossing over in the male. Purple vestigial flies mated to red-eyed, long-winged flies gave red-eyed, long-winged F_1 males and females. When these F_1 males were bred to purple vestigial females only two classes were produced:

Red Long.	Purple Long.	Red Vestigial.	Purple Vestigial.
52	0	0	62
141	0	0	113
96	0	0	131
28	0	0	34
68	0	0	89
22	0	0	33
112	0	0	90
519	0	0	552

The result is explicable if no crossing over occurs in the male and the analysis is the same in principle as that for the black vestigial case. As explained before, every sperm contains one or the other recessive since they went in separately and have not crossed over in the male.

When the F_1 females (sisters to the males just tested) were mated to purple vestigial males, the following results were obtained:

Red Long.	Purple Long.	Red Vestigial.	Purple Vestigial.
2,876	270	270	2,433

The result is explicable on the hypothesis of crossing over (about ten per cent.) in the female, as the analysis for the comparable case for black vestigial shows.

Purple-eyed, long-winged flies were mated to red-eyed, vestigial flies, and gave normal F_1 flies. When the F_1 males were bred to purple vestigial females the following results were obtained:

Red Long.	Purple Long.	Red Vestigial.	Purple Vestigial.
0	62	42	0
0	78	70	0
0	61	53	0
0	66	103	0
0	79	90	0
0	346	358	0

Here again the results are explicable on the hypothesis of non-crossing over in the male. The recessives enter the F_1 male from opposite sides, *i. e.*, they lie in different but homologous chromosomes. Hence if no crossing over occurs in the male each spermatozoon will contain one or the other recessive, and since the eggs are all alike and carry only double recessive factors only two types of zygotes are expected.

When the F_1 females, sisters to the males just tested, were likewise bred to purple vestigial males, the following classes result:

Red Long.	Purple Long.	Red Vestigial.	Purple Vestigial.
265	2,203	2,038	234

Crossing over in the female (about 10 per cent.) explains the classes that appear in this experiment.

These results with purple vestigial are comparable at every point with those for black vestigial and both furnish evidence of no crossing over in the male. The numbers are large enough to make it highly probable that crossing over in the male did not occur.

Further Examples of Non-crossing over in the Male Between Genes in the Second Pair of Chromosomes.

The following data are taken from experiments that Mr. C. B. Bridges and the author are carrying out. The records have been made by Mr. Bridges. A recessive mutant called "dachs" (from the short legs of the flies) was combined with another character also in the second group, viz., black. When the double recessive dachs black is crossed to the wild (normal gray) fly

the offspring are normal. When an F_1 male was mated to dachs black females the following results were obtained:

Normal Gray.	Dachs Gray.	Normal Black.	Dachs Black.
98	0	0	72

These results are consistent with the hypothesis of no crossing over in the male. Since dachs lies on the other side of black from purple and vestigial, the data extend the application to a new section of the second chromosome, and considerably increase the significance of the results.

Another recessive mutant stock has wings curved in an arc. "Arc" was combined with black—both belonging to the second group of factors. When black arc was mated to wild flies (with straight wing) the offspring were normal. An F_1 male back crossed to black arc gave the following results:

Gray Straight.	Black Straight.	Gray Arc.	Black Arc.
161	0	0	145

This result also is conformable with the hypothesis of no crossing over in the male, and since arc lies on the same side of black as does purple and vestigial but considerably beyond either, still a new section is found to be free from crossing over in the male. Further, since in the female there is a very great amount of crossing over (about 36 per cent.) between black and arc, the lack of crossing over in the male is even more striking.

When black was crossed to purple the F_1 flies were gray red. An F_1 male was mated to a black purple female and gave in the next generation:

Gray Red.	Black Red.	Gray Purple.	Black Purple.
0	74	71	0

These results are again conformable with the hypothesis. In this case the two recessives entered from different sides.

Another mutant caaracter, streak, is a dominant. Streak gray mated to normal (thorax) black gave streak gray F_1 flies. An F_1 male was mated to the double recessive, normal black females, and gave the following classes:

Streak Gray.	Normal Gray.	Streak Black.	Normal Black.
19	0	0	21

Again the results conform. Here the two dominants entered from one side and two recessives from the other, and the double recessive normal black was used for testing the gametes of the F_1 male. Streak lies at the most extreme end of the chromosome so far as known, on the same side of black as does dachs, and on the other side from purple, vestigial and arc. The interval between streak and black is nearly as long as that between black and arc, so that the results are of interest because the whole section from streak on the one hand to arc on the other is known to give the same result, namely, a complete absence of crossing over. These two loci, streak and arc, are so far apart that in the female there is practically free Mendelian assortment.

No Crossing over in the Male between Genes in the Third Pair of Chromosomes.

A test of whether or not crossing over takes place in the male between genes in the third group; or, as we say, in the third chromosome, was first published for the case of pink and ebony by Sturtevant (*Science*, 1913), who showed that no crossing over occurred in the F_1 male for the small number of males tested. The following case gives similar results for another pair of loci. The data are taken from experiments that are being carried out by C. B. Bridges and the author.

A mutant stock has kidney-shaped eyes. A double recessive stock of pink kidney was made up, both factors being in the third chromosome. Pink kidney mated to wild flies gave F_1 flies with red round eyes. The F_1 males back crossed to pink kidney females gave the following results:

Red Round.	Pink Round.	Red Kidney.	Pink Kidney.
23	0	0	15
11	0	0	9
56	0	0	50
91	0	0	61
6	0	0	8
22	0	0	17
11	0	0	5
6	0	0	2
63	0	0	58
142	0	0	114
431	0	0	339

These results are in harmony with the hypothesis of no crossing over in the male between genes in the third group of chromosomes. The amount of crossing over between pink and kidney in the female is about 15 per cent., which is greater than the most frequent value of about 5 per cent in Sturtevant's case of pink ebony.

Discussion.

In their paper of 1911, Bateson and Punnett described certain phenomena that they called coupling and repulsion. The numerical and class results offer many points of similarity to the cases here described. In a later paper they gave reasons for abandoning the earlier view of repulsion as distinct from coupling. In this paper (December, 1911) they gave two cases in which linkage occurs, but in which crossing over must be assumed to take place in both sexes. Bateson and Punnet postulate in order to account for their results that segregation takes place at some early stage in the germ-tract. Whatever form of interpretation may apply to the cases described by Bateson and Punnett, the tests that I have made of F_1 males and females show, that in *Drosophila* at least, the results are due to failure of crossing over between factors in one sex. It may be that in certain animals and plants crossing over is the same in both sexes, while in other cases it may be that crossing over is different in the two sexes. Whether this is true or not can only be determined by making tests like those here employed. Until such tests have been made for other forms in which linkage has been found we cannot know how widely the explanation here followed may be extended.